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Nesting Ecology of the Redhead Duck on Knudson Marsh, Utah

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NESTING ECOLOGY OF THE REDHEAD DUCK ON KNUDSON MARSH, UTAH

by

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Thomas Claud Michot

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ABSTRACT

Nesting Ecology of the Redhead Duck on

Knudson Marsh, Utah

by

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Utah State University, 1976

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Redhead duck (*Aythya americana*) nesting and habitat change was studied in Knudson Marsh, Utah, in 1974 and 1975, and compared with earlier studies from 1950 and 1955 on the same marsh. Water conditions in 1975 were found to be similar to those in 1950, both years of favorable habitat, yet there was a decline in numbers of redheads from 500 pairs in 1950 to 50 pairs in 1975. The number of nests found also declined from 151 in 1950 to 49 in 1975. Water conditions were poor in 1955 and slightly more favorable in 1974, but there was a decline from 95 pairs and 49 nests in 1955 to 50 pairs and 23 nests in 1974. Success of active nests was greater in the present study than in 1950, but hatching success in successful nests was greater in 1950. No appreciable change in the vegetational composition of the marsh was detected between 1950 and the present study.

(61 pages)

INTRODUCTION

Knudson Marsh (Figure 1) is located in the Salt Lake Valley of Utah, an area which has been considered one of the most productive redhead (*Aythya americana*) breeding grounds in the United States (Williams and Nelson 1943). Wingfield (1951) and Weller et al. (1958) studied Knudson Marsh and thereby provided a basis for comparative research in the 1970's. Changes in the redhead population could therefore be detected, and the habitat assessed to determine a basis for population fluctuations.

Knudson Marsh is located 3.2 kilometers west of Brigham City, Utah (sections 29-37, T. 9N., R. 2 W., SLM), and is surrounded by salt flats. Unit 5 of the Bear River Migratory Bird Refuge lies 2.4 kilometers south of Knudson Marsh, and the nearest road is 2.4 kilometers to the north, thus isolating the study area and virtually eliminating human disturbance during the breeding season. Cattle graze the surrounding vegetation in the summer, and hunting and trapping takes place on the marsh in the fall and winter.

Knudson Marsh is privately owned, 101 hectares in size, and is divided into an upper marsh of 70 hectares, and a lower marsh, the two being connected by several channels and separated by salt flats (Weller et al. 1958). This study, as the two previous ones, deals only with the

Figure 1. Knudson Marsh, Box Elder County, Utah, 1975.

upper marsh. Detailed descriptions of the study area can be obtained from Wingfield (1951) and Weller et al. (1958).

The water level in Knudson Marsh is determined by the amount of water coming into the marsh from Black Slough on the north, and by the amount of water flowing out of the marsh on the south end. The incoming water comes from melted snow from the Wellsville Mountains, as well as local precipitation. The earthen dike on the south end of the lower marsh has two large culverts through which water leaves the marsh to flow into Reeder Channel and south to Unit 5 of the Bear River Migratory Bird Refuge. These culverts can be blocked to regulate the outflow of water from the marsh. Because the marsh is privately owned, and not managed for waterfowl use to any great extent, the water level fluctuates from week to week, and the conditions vary from one year to the next.

The high duck nesting densities found at Knudson Marsh in the 1950's were second only to island nesting situations. This was attributed to the marsh's island-like setting, there being a channel which almost completely surrounds the vegetation in the marsh, as well as the fact that the water is well interspersed with vegetation. Even so, there was a drastic decrease in waterfowl production from 1950 to 1955, due to drought and grazing (Weller et al. 1958). This study was undertaken to determine what changes have taken place since then and to hopefully give some insight as to the causes of these changes.

The primary objectives of this study were:

1. To determine the breeding population densities of redheads on Knudson Marsh.

2. To determine population trends by comparing this study with previous studies.

3. To determine the factors involved, productivity changes and their effects on the population.

As the study progressed, the following hypothesis was set up: the redhead population of Knudson Marsh has declined due to changes in habitat.

LITERATURE REVIEW

Nesting Studies

According to Weller (1964), redheads originated in the alkaline water of the southwestern United States, and only recently has the breeding range spread to include the prairie pothole region of the northern U. S. and southern Canada. Redheads have been studied throughout their breeding range since the early part of this century. Early nesting studies were made by Wetmore (1921) in Utah and Weydemeyer (1933) in Montana. A more intensive nesting study was made at the Bear River Migratory Bird Refuge by Williams and Marshall (1938), followed by an unpublished report on the management of the species in Utah (Williams and Nelson, 1943).

While these studies were taking place in Utah, the redhead was also being studied in Iowa, first by Bennett (1938) and then by Low (1940), who later published the first monographic study of the species (Low 1945). Mendall (1945) reported redheads breeding in New Brunswick, which was the first record of such in any of the maritime provices. The redhead population in southern Manitoba, however, was thought to be seriously declining (Hochbaum 1946) at this time, despite excellent environmental conditions.

The first waterfowl study on Knudson Marsh was made in 1950 (Wingfield 1951; Wingfield and Low 1955), when the productivity of mallards (Anas platyrhynchos), cinnamon teal (Anas cyanoptera), ruddy duck (Oxyura jamaicensis), and redheads was studied. That study was followed up in 1955 by Weller et al. (1958) and by the present study.

Duck production was studied at Gray's Lake in southeastern Idaho from 1949 to 1951 (Steel et al. 1956), and at Tule Lake and Lower Klamath National Wildlife Refuges in northern California, one of the major western redhead breeding areas (Miller and Collins, 1954). This northern California study was followed up by Rienecker and Anderson (1960), who monitored the change in production that occurred in 5 years. Lokemoen (1966) studied the redhead population of the Flathead Valley area in western Montana.

Olsen (1964) investigated canvasback and redhead breeding populations in Manitoba, where the breeding ranges of these two species overlap. Keith (1961) studied waterfowl ecology on small impoundments in southern Alberta. Waterfowl production in the prairie pothole region was also studied by Stoudt (1971) in Saskatchewan and Smith (1971) in Alberta. The adaptability of the redhead in nesting situations was shown by McKnight (1974), who found many redheads nesting on dry land in Utah, and Williams (1975), who found redheads breeding as far south as Jalisco, Mexico.

Population and Movement Studies

Banding operations at Bear River Migratory Bird Refuge in Utah as early as the 1920's and 1930's resulted in papers on redhead migration by Williams (1944), Van Den Akker and Wilson (1949) and Hickey (1952). Brakhage (1953) studied migration and mortality of ducks banded at Delta, Manitoba, while similar studies were made by Weller and Ward (1959) on hand-reared redheads and Bensen and DeGraffe (1958) on redheads banded in New York.

Weller's (1964) paper is probably the most complete study to date on redhead distribution and migration; banding data were utilized, as well as data from population cansuses on the breeding and wintering grounds. Robbins (1949), Lensink (1964) and Rienecker (1968) also published studies based on band recoveries. The effect of restrictive hunting regulations on canvasbacks and redheads was studied by Geis and Cooch (1972). Additional information on redhead population status and life history is presented in Bellrose (1976).

Redheads on their wintering grounds were studied by Heit (1948) and Kiel (1957): Low (1941) studied the birds during their spring migration. Sex and age ratios were investigated by Bellrose et al. (1961). Thornburg (1973) studied diving duck movements on an upper Mississippi River pool, and brood movements in Manitoba were studied by Evans et al. (1952).

Anatomical, Physiological and Behavioral Studies

Weller (1957) completed a comprehensive paper on the growth, weights and plumages of the redhead, and Ryan (1972) studied body weight changes of wintering diving ducks. Dane and Johnson (1975) investigaged a method of age determination of female redheads from wing feather examinations and measurements. Age and sex identification from wing plumages was also presented in a key by Carney (1964).

Redhead nest parasitism was reported by Friedmann (1932), Erickson (1948) and McKinney (1954). Weller (1959) did a monographic study on redhead parasitism, using data gathered at Knudson Marsh, Utah, and southern Manitoba.

Dzubin (1955) reported on home range in waterfowl, and Oring (1964) studied postbreeding behavior. Weller (1965) published a paper on the chronology of pair formation in redhead and scaup. Smart (1962) studied biological problems involved in the restocking of redheads and Bensen and Browne (1973) studied the establishment of breeding colonies of redheads by releasing hand reared birds.

Food habits of adult and juvenile diving ducks were studied by Bartonek and Hickey (1969a and b). Sugden (1969) studied food selection and energy requirements in Alberta. Food habits were also investigated by Bergman (1973), who studied postbreeding canvasbacks and redheads, and McMahan (1970), who studied redheads on their Texas wintering grounds. General information on redhead behavior, anatomy and life history is presented in Johnsgard (1975) and Bellrose (1976).

METHODS

Breeding Population Censuses

Aerial counts were made on 2 June 1974, and 22 May and 11 June 1975, to estimate the breeding population of redheads on Knudson Marsh. These counts were made from a Cessna 150 at about 90 to 150 meters above the marsh; ground counts were conducted in the early part of the breeding season.

Nesting Survey

The emergent vegetation was systematically searched in 1974 to locate nests of redheads, mallards, cinnamon teal, and ruddy duck. An additional search was made for redhead nests in 1975. Each nest found was marked with a cane (*Phragmites australis*) placed five feet north of the nest. The inflorescence of the cane was usually visible above the cover vegetation, and a piece of paper tape with the number of the nest on it was placed around the culm.

The following data were recorded for each nest found: nest number, duck species, date and time found, vegetation type, height and density of vegetation, water depth, height of the nest over water, amount of down present, degree of concealment, number of host eggs and parasitic eggs, flushing distance, and distance of the nest from open water.

The nests were visited periodically to determine the number of eggs and the fate of the nest.

Water Levels

Water level fluctuations were monitored from a graduated marker on the north end of the marsh. Records were kept throughout the breeding season for both years.

Records of the water flow of the Bear River at the Collinston, Utah, guaging station were obtained from the U. S. Geological Survey. These records were useful in comparing the available water supply of the four years of study: 1950, 1955, 1974 and 1975.

Vegetation Analysis

A vegetation analysis was made in 1974 by grid point sampling to estimate the percent cover of each species and the ratio of open water to vegetation. The dominant vegetative cover was recorded every 25 paces along 31 north-south transects, which were 25 paces apart. A cover map was made from aerial photographs in order to study the change in habitat between 1950 and 1975. A diversity index (Pielou 1975) was conducted on each map.

Previous Studies

Uncited data used in this paper from 1950 were taken from Wingfield (1951) and Wingfield and Low (1955). Data from 1955 are from Weller et al. (1958) and Weller (1959). Results from all four years of study are not presented in every section because data may have been lacking from one or more years.

RESULTS

Habitat Change

Water levels

Annual fluctuations in the flow of the Bear River at the Collinston, Utah gauging station from 1931 to 1975 are shown in Figure 2. Although Knudson Marsh does not obtain its water from the Bear River, this graph gives an indication of the annual variation in water conditions of the area. The water flow in 1950 (1,642,000 acre/feet) was higher than any of the other three years of study, and was well above the 45 year average (1,168,000 acre/feet). Since the water conditions in the late 1940's were favorable, Knudson Marsh in 1950 had plenty of dense emergent vegetation and plenty of water, thus producing excellent redhead nesting habitat.

After 1952, however, water conditions declined drastically and in 1955, the third year of drought, the marsh habitat was in poor condition. Water conditions after 1955 varied greatly, with a peak in 1971. By 1974, the third year of study at Knudson Marsh, the Bear River flow was still quite high. The dike below the marsh, however, had been damaged and the water level in the marsh dropped quite rapidly after the spring thaw. The dike was repaired late in the summer of 1974, after the ducks had finished nesting. The Bear River flow in 1975 was good,

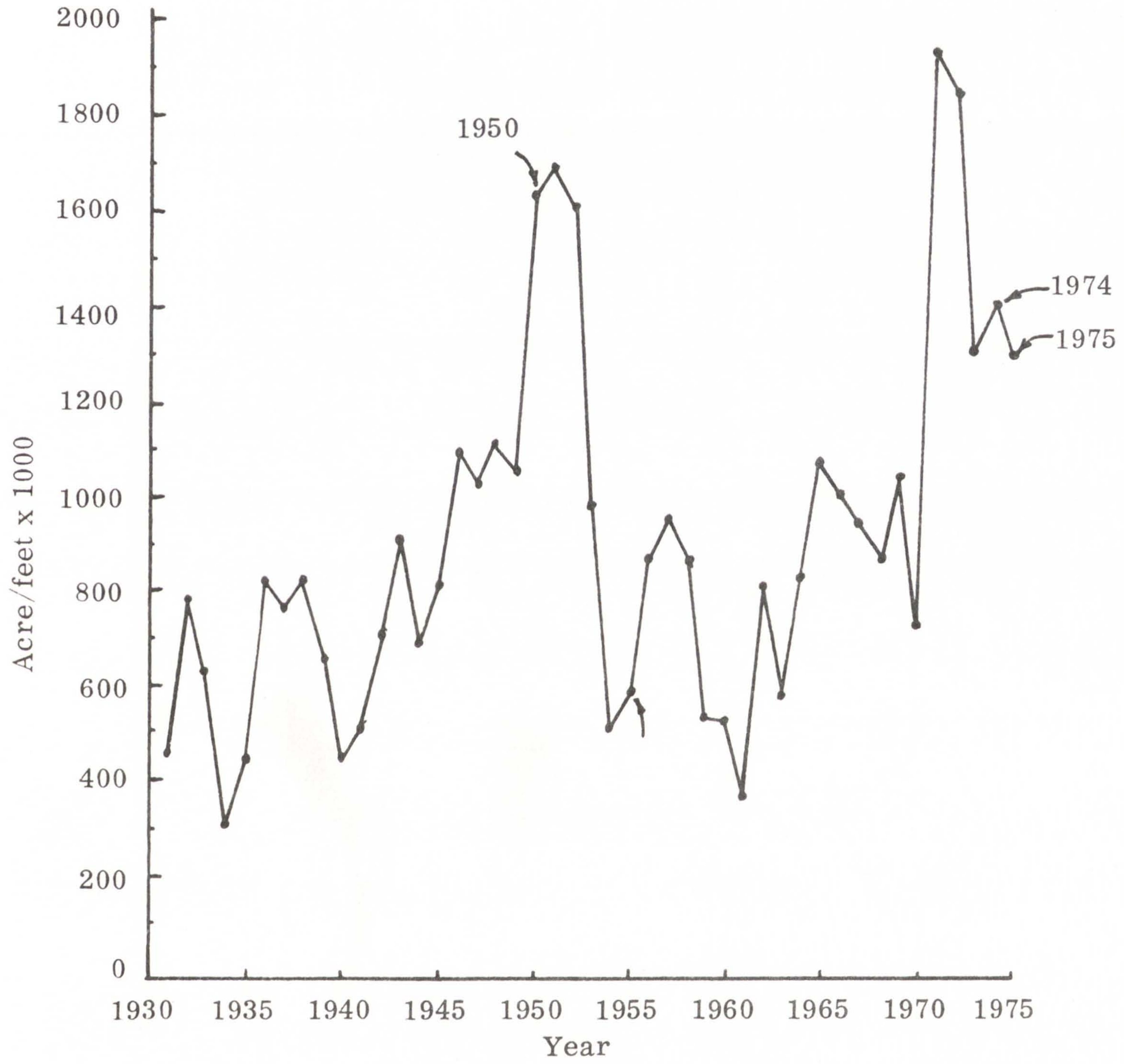

Figure 2. Annual discharge in acre-feet of the Bear River near Collinston, Utah (from US Geological Survey records).

and the water conditions at Knudson Marsh were also good, as the water was retained by the repaired dike.

In April, 1950, there were 2 to 30 cm of water in the marsh vegetation. By late May and early June the vegetation in the northern portion of the marsh was no longer inundated, but the channels and open ponds were still full of water, and the southern portion of the marsh had 2 to 15 cm of water in the vegetation. Most of the redhead nests were constructed over 1 to 8 cm of water (Table 1), and cattle seldom entered the marsh. The hardstem bulrush (Scirpus acutus) reached 2 to 3 meters in height and became so dense that it was almost impossible for a man to walk through it.

In 1955, the shallow ponds and channels in Knudson Marsh were dry by late May, and the water level in the main pool had receded drastically by early July. Only one nest was constructed over water (Table 1), and cattle had entered the marsh by April. The hardstem bulrush never reached 2 meters in height except on the borders of channels and potholes, and it was relatively easy to walk through, being less dense than in 1950 and having been thinned out even more by cattle. The new growth of vegetation was not dense enough to change the general appearance of the marsh from brown to green.

The marsh vegetation was covered with 1 to 8 cm of water in late March, 1974, but by the end of April the water was gone from most of the vegetated areas. By late May, most of the shallow ponds and potholes were dry, and the main pool was mostly exposed mud flats by

Table 1. Depth of water under redhead nests, Knudson Marsh, Utah.

Variable	Percent of nests 1950	1955	1974	1975
No water	24	98	100	4
1-8 cm	60	2	0	46
9-16 cm	14	0	0	21
17-34 cm	2	0	0	29
Total nests	122	42	23	28

late June. No redhead nests were constructed over water (Table 1). The water conditions in the marsh seemed to be almost as poor as in 1955, but the cattle did not enter the marsh until late June and the hardstem bulrush was quite tall (up to 2.5 meters) and dense, and the marsh had a lush green appearance. Apparently the favorable conditions in the early 1970's enabled the vegetation to retain its vigor through 1974, whereas the drought years in the early 1950's severely curtailed the vegetative growth by 1955.

Through most of the 1975 breeding season the marsh retained 1 to 30 cm of water in the vegetation, and the channels and potholes never dried up. Most of the redhead nests were constructed over 1 to 16 cm of water (Table 1), and the cattle never entered the marsh. The hardstem bulrush grew up to 2 to 3 meters high and was very dense. The water level was maintained by controlling the outflow of water through the culverts on the south end of the marsh.

Vegetation

The ratio of open water to total vegetation in Knudson Marsh increased slightly from 1950 to 1974 (Table 2), but this change is not believed to have had any effect on the redhead nesting ecology. The ratio for both years is close to the 35:65 ratio which Williams and Nelson (1943) found to be the preferred water:cover ratio for redheads in Utah. The changes in open water and vegetation are shown in the cover maps from 1950 (Figure 3) and 1975 (Figure 4).

Table 2. Vegetation changes on Knudson Marsh, Utah.

Variable	1950	1974
General type:	% of total marsh area	
Open water	31.0	37.8
Vegetation (all spp.)	69.0	62.2
Vegetation type:	% of total vegetation	
Hardstem bulrush	56.2	58.0
Olney bulrush	24.1	21.1
Alkali bulrush	0.8	0.0
Cattail	12.4	2.0
Saltgrass	6.5	18.6
Cane	0.1	0.2
Total	100.1	99.9

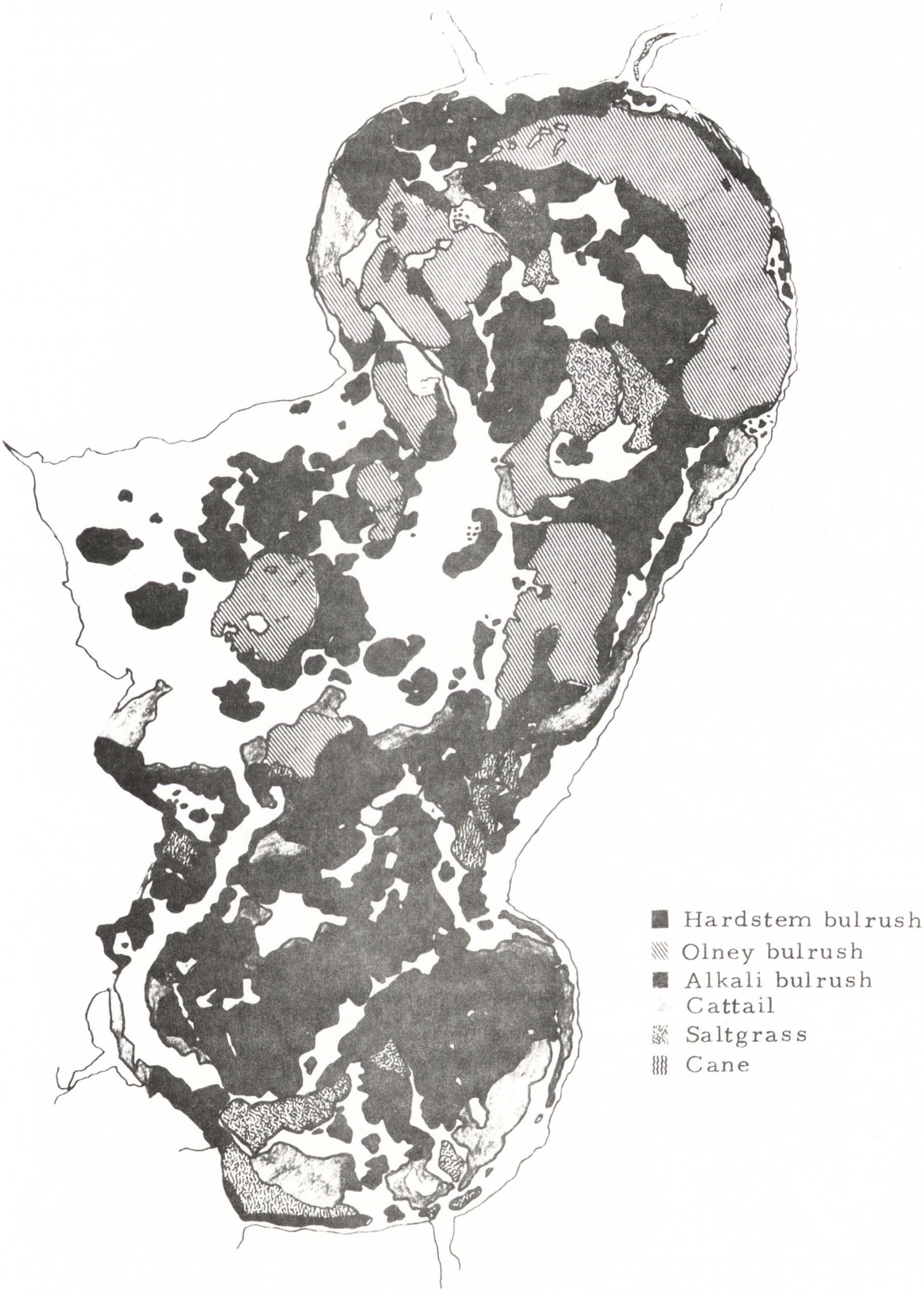

Figure 3. Knudson Marsh, Utah, 1950, showing cover types and open water (from Wingfield 1951).

Figure 4. Knudson Marsh, Utah, 1975, showing cover types and open water.

Hardstem bulrush, the favored cover species for nesting redheads (Williams and Marshall 1938; Williams and Nelson 1943; Wingfield 1951; Bellrose 1976), seemed to be present in about the same proportion in 1974 as in 1950 (Table 2). The only major differences in the species composition of the cover were the increase in saltgrass (Distichlis spicata) and the decrease in cattail (Typha latifolia). Neither of these two species have been shown to be important as redhead nesting cover on Knudson Marsh.

Wingfield (1951) reported competition between hardstem bulrush and cattail on Knudson Marsh and that the latter was being invaded by the former. He also noted an increase in cattail on the southern portion of the marsh, on areas which were bare of vegetation in 1937, citing deeper water as the cause for this change. Bolen (1964), however, found that water depth creates differences between open water and vegetated areas, but not between different vegetation zones, and that soil salinity is more closely correlated with vegetational zonation. In addition, it has been found that cattail only germinates on mud flats which have been exposed for at least 24 hours (A. H. Holmgren, personal communication).

The cattail was probably replaced in different areas of the marsh between 1950 and 1974 by saltgrass, hardstem bulrush, and open water. The fact that alkali bulrush (S. paludosus) is now non-existent on Knudson Marsh (Table 2) supports Bolen's (1964) contention that it is a pioneer species which is usually superseded by other emergent vegetation due to reduced salinity or intrusion by other salt tolerant species.

The two small clumps of cane present in 1950 were still in the same locations at the time of this study and no change was detected. The percentage of Olney bulrush (*S. olneyi*) also showed no change during the 24 hour period (Table 2). There was no apparent change in vegetational zonation from 1950 to 1955 (Weller et al. 1958).

A diversity index (Pielou 1975) did show a significant difference ($w = 38$, $p < 0.032$) by a Wilcoxon rank sum test (Hollander and Wolfe 1973) between the 1950 and 1975 maps (Figures 3 and 4). This difference in diversity was not believed to have affected redhead nesting to any great extent, but reflects subtle changes in the marsh composition.

Other vascular plants found on Knudson Marsh during the 1974 vegetation survey are listed in Table 8 (Appendix). The submerged aquatics, pondweed (*Potomogeton pectinatus*) and widgeongrass (*Ruppia maritima*), were much more numerous in 1975 when there was deeper water in the marsh; in 1974 submersed aquatics were extremely rare. The non-dominant terrestrial species formed the main components of the understory vegetation. I believe these species were present in great numbers only during dry years when there was no standing water in the vegetation.

Breeding Populations

The redhead population of Knudson Marsh at the time of this study declined markedly from what it was in the early 1950's (Table 3). The present study took place during two years of extreme water conditions, 1974 and 1975, which correspond closely to the conditions of 1955 and 1950, respectively. It would seem appropriate, therefore, to compare the populations of years of similar habitat conditions, i.e., to compare 1950 with 1975 and 1955 with 1974, to determine if there has been a long term change in the population.

Table 3. Redhead data from Knudson Marsh, Utah.

Variable	1950	1955	1974	1975
Redhead breeding pairs	500	95	50	50
Redhead nests	151	49	23	49
Average eggs hatched[a] per redhead nest	3.9	--	2.4	1.9
Average eggs hatched[a] per hectare	6.8	--	0.8	1.3

[a]Includes parasitic redhead eggs hatched in nests of other species.

The fact that the breeding populations of 1974 and 1975 were the same, yet the number of nests increased from 23 to 49, can be explained in that nesting is more easily influenced by local conditions. When the birds arrived early in the breeding season in 1974, the marsh was in fairly good condition. The water level dropped rapidly, however, thus curtailing the nesting of many hens. Birds were present in 1974, but they did not nest to the extent that they did in 1975 when the water conditions were more favorable.

During the two years of favorable conditions on the marsh, 1950 and 1975, the breeding population decreased from 500 to 50 pairs (90 percent decrease) and the number of nests decreased from 151 to 49 (67 percent decrease). In the unfavorable years, 1955 to 1974, the population dropped from 95 to 50 pairs (47 percent decrease) and from 49 to 23 nests (53 percent decrease). Treating these four years as being representative of a long term trend, it is apparent that the redhead population of Knudson Marsh has undergone a decline in this 26 year period which cannot be related to habitat changes.

Nest Characteristics

Cover types

Hardstem bulrush was found to be the preferred nesting cover species for redheads during 3 years of study (no data are available from 1955) at Knudson Marsh (Table 4). During 1950 and 1974, when the marsh vegetation was systematically searched for nests, 75 percent and 70 percent of the nests, respectively, were found in hardstem bulrush, which comprised less than 60 percent of the total vegetation. In 1975 this cover type was searched to a much greater extent than other types.

Cattail and saltgrass were utilized rarely in 1950, and not at all in 1974 and 1975. Olney bulrush was found to be a secondary cover type.

Distance from open water

Redhead nests appear to have been closer to open water (X^2 = 22.4, d.f. = 4, $p < 0.005$) in the present study than in 1950 (Table 4). No nests were found farther from open water than 9 meters in 1975 and 23 meters in 1974; in 1950, however, nests were found at 30+ meters from open water.

Table 4. Data from redhead nests in relation to cover type and open water, Knudson Marsh, Utah.

	% of nests		
Variable	1950	1974	1975
Cover type:			
Hardstem bulrush	75	70	97
Olney bulrush	20	30	3
Cat tail	4	0	0
Saltgrass	1	0	0
Total nests	125	23	36
Distance from open water:			
0.0 - 1.8 m	8	26	25
2.1 - 4.6 m	15	22	36
4.9 - 7.6 m	26	13	11
7.9 -15.2 m	38	31	28
15.5 + m	13	9	0
Total nests	125	23	36

It is advantageous for a redhead hen to construct her nest close to open water to facilitate easy escape when disturbed. In 1950, when redhead densities were quite high, there may have been competition for nest sites close to open water, and many nests had to be constructed in less favorable sites, at a greater distance from open water. In 1974 and 1975, however, with much smaller numbers of redheads nesting, a greater percentage of hens were able to secure a favorable nest site close to open water.

Clutch size

The average redhead clutch sizes for the 3 years of study are fairly similar (Table 5). The figures shown represent the maximum number of eggs associated with each nest, including eggs outside of the nest and in the water around the nest. This deviates from the standard definition of clutch, which includes eggs laid by only one female. The wide range in the numbers of eggs per clutch may be due to the large occurrence of intraspecific parasitism.

Redhead clutch sizes reported in the literature have averaged from 8.6 (McKnight 1974) to 13.8 (Miller and Collins 1954). Williams and Nelson (1943) examined 918 nests in Utah, and found a mean clutch of 10.5 eggs, with a range of one to 39. Williams and Marshall (1938) found that 343 nests on the Bear River Refuge averaged 12.5 eggs, with a maximum clutch of 39. Weller (1959), however, believes that the true clutch of the redhead is smaller. He found that 17 unparasitized redhead nests averaged 7.3 eggs, ranging from five to nine.

Table 5. Clutch sizes in redhead nests, Knudson Marsh, Utah.

Variable	1950	1974	1975
Average clutch	13.5 ± 0.7	12.5 ± 1.4	12.8 ± 1.3
Range	1-50	3-28	2-44

Reproductive Success

The redhead's unusual reproductive behavior, which results in nest parasitism, seems to lower the reproductive success (Weller 1959). This is due to the fact that many redhead parasitic eggs are never incubated. Often dump nests are deserted, or parasitic eggs are laid after the host has already started incubating their eggs, thus they hatch before the parasitic eggs are fully incubated.

The success of redhead nests from three years at Knudson Marsh is shown in Table 6. Data are not presented from 1955 because Weller believed the redhead productivity was affected by his activities in the marsh, including nest trapping and daily disturbances to the nests (M. W. Weller, personal communication).

Table 6. Redhead egg and nest data from Knudson Marsh, Utah.

Variable	1950		1974		1975	
	Sample size	% hatch or successful	Sample size	% hatch or successful	Sample size	% hatch or successful
Total redhead nests	151	--	23	--	49	--
Redhead nests active when found	125	30.4 ±4.1	13	53.8 ±13.8	23	56.5 ±10.3
Redhead nests of known fate	122	31.1 ±4.2	23	30.4 ±9.6	46	28.3 ±6.6
Successful redhead nests	38	--	7	--	13	--
Total redhead eggs in redhead nests	--	--	276	18.1 ±2.3	628	12.1 ±1.3
Redhead eggs in successful redhead nests	482	72.8 ±2.0	82	61.0 ±5.4	204	37.3 ±3.4
Redhead eggs in active when found redhead nests	1629	21.8 ±1.0	163	30.7 ±3.6	293	25.9 ±2.6
Total redhead eggs in all nests[a]	3672	13.1 ±0.5	319	17.2 ±2.1	726	12.3 ±1.2
Redhead eggs hatched[a]	480	--	55	--	89	--

[a]Includes redhead eggs from redhead nests plus redhead eggs laid in nests of other species.

Nesting success

The nest successes for redhead nests of known fate seem to be very close for the three years. The percent of active nests which were successful, however, appears to have increased significantly since 1950. The reason for this increase is not readily apparent, but it is possible that there was a higher incidence of intraspecific parasitism in 1950, as evidenced by the high average clutch of 13.5 (Table 5). This high intraspecific parasitism resulted in a high nest desertion rate; thus a smaller percentage of nests was successful. The greater incidence of predation in 1950 may have also contributed to the low nest success.

Predation was found to be a limiting factor to nest success in 1950, but not in the present study. Thirty nests (24.6 percent of total redhead nests) were lost to predation in 1950, primarily by California gulls (*Larus californicus*) and striped skunks (*Mephitis mephitis*). The success of active nests which were not preyed upon was 41.3 percent, still slightly lower than the successes for 1974 and 1975. Nine redhead nests in 1974 had been preyed upon, but six of these were deserted when found, so they may have been preyed upon after the hen had already deserted the nest. The other three nests (13.0 percent of total redhead nests) were believed to have been deserted due to predation. Only one redhead nest in 1975 had been preyed upon, and it had already been deserted when found.

Many redhead nests in the present study had been deserted when found, especially during the early part of the nesting season. Most of these desertions can undoubtedly be attributed to the redhead's weak reproductive habits (Weller 1959). Many deserted nests contained a small number of eggs. These may have been deposited by semiparasites before they began construction of their own nests, and were never incubated. Other nests with large clutches were probably deserted as a result of disturbance during intraspecific parasitism.

Redhead nesting success, as reported in the literature, is quite variable, ranging from 15 percent (Lokemoen 1966) to 88 percent (Rienecker and Anderson 1960). This variability is probably due primarily to the parasitic behavior of this species. The success at Knudson Marsh obviously falls somewhere between these extremes, and it is impossible to draw any conclusions by comparing the nest success of this population with that of other redhead populations in North America.

Hatching success

The hatching success of redhead eggs in successful nests shows a significant decrease between the 1950 study and the 1974 and 1975 studies (Table 6). The reason for the low hatching success in 1975 is probably that a large number of eggs were laid in nests which were deserted due to intraspecific parasitism or were never incubated. There was one nest in 1975 which contained a total of 44 eggs, obviously from more than one hen. The nest was incubated, though, and one egg hatched. This probably biased the hatching success of that year to some extent.

The hatching success in 1950 is significantly higher than those of the present study, although the nesting success for that year appears to be the same as or lower than those of the present study. The reason for this discrepancy is not fully understood, and cannot be explained with the data available from this study.

Productivity

The composition of Knudson Marsh, plus the belief that many hens moved their broods off the marsh to be reared (Wingfield and Low 1955), made accurate brood counts virtually impossible. The only estimate of production available, therefore, is the number of eggs that hatched. The change in total marsh production from year to year, as would be expected, was directly proportional to the change in numbers of nests found (Table 6).

The production of redheads expressed in eggs hatched per hectare (Table 3) shows a drastic decrease from 6.8 in 1950 to 0.8 and 1.3 in 1974 and 1975, respectively. This is to be expected, since there were fewer birds on the marsh during the present study, and fewer nests. Perhaps a better expression of productivity is the number of eggs hatched per redhead nesting effort. The fact that this figure also shows a decline from 3.9 to 2.4 and 1.9 (Table 3) indicates a true change in productivity. The standard deviations for 1974 and 1975 are 0.7 and 0.4, respectively, but insufficient data are avilable from 1950. Consequently, the significance of this apparent decline in productivity could not be assessed. The average number of eggs hatched per active redhead nest was 3.9 for 1950 and 4.2 and 3.9 for 1974 and 1975. This implies that the productivity has not changed.

Interspecific Parasitism

The primary hosts for redhead nest parasitism in Knudson Marsh were mallards and cinnamon teal, mainly because they were the most abundant. Ruddy ducks, which nested in small numbers on Knudson Marsh, were also parasitised to some extent. Canvasbacks (Aythya valisineria), which are important as host species in other areas, do not usually nest in the Knudson Marsh area. Although mallards and cinnamon teal are both known as upland nesters, they construct over-water nests quite frequently in Knudson Marsh. This makes them acceptable hosts to parasitic redheads.

The data from mallard and cinnamon teal nests are presented in Table 7. Search efforts in 1975 were concentrated in the hardstem bulrush habitat, thus many dabbler nests constructed in other cover types were undoubtedly not located.

Apparently a greater percentage of mallard nests were parasitized in 1975 (84.6 percent) than in the other study years, but parasitism of cinnamon teal nests was greatest in 1950 (75.9 percent). The percent of nests of both species parasitized was lowest in 1974 (36.2 percent)

Table 7. Data from mallard and cinnamon teal nests, Knudson Marsh, Utah.

Variable	Mallard				Cinnamon teal				Total			
	1950	1955	1974	1975[a]	1950	1955	1974	1975[a]	1950	1955	1974	1975[a]
Number of nests	390	171	13	13	172	57	34	20	562	228	47	33
% nests parasitized by redhead	69.5 ±2.6	68.0 ±4.0	23.1 ±11.7	84.6 ±10.0	75.9 ±3.6	53.7 ±7.8	41.2 ±8.4	40.0 ±11.0	71.4 ±2.1	49.6 ±3.8	36.2 ±7.0	57.6 ±8.6
% host eggs hatched	58.9 ±0.9	--	64.5 ±5.5	38.3 ±6.3	40.8 ±1.7	--	46.6 ±3.1	21.8 ±4.7	55.1 ±8.2	--	50.8 ±2.8	29.0 ±3.9
% redhead eggs hatched	5.9 ±0.6	--	33.3 ±13.6	16.4 ±5.0	6.5 ±0.9	--	2.9 ±2.8	9.5 ±4.5	6.1 ±0.5	--	10.9 ±4.6	13.4 ±3.5
% nests successful	65.7 ±2.6	67.3 ±4.5	60.0 ±15.5	50.0 ±14.4	35.7 ±4.0	34.1 ±7.4	51.6 ±9.0	27.8 ±10.6	56.3 ±2.3	58.3 ±4.0	53.7 ±7.8	36.7 ±8.8
% unparasitized nests successful	64.0 ±4.8	66.0 ±7.7	62.5 ±17.1	100.0	41.0 ±8.4	44.0 ±11.7	47.1 ±11.4	30.0 ±14.5	58.3 ±4.3	58.9 ±6.6	51.9 ±9.6	36.4 ±14.5
% parasitized nests successful	66.4 ±3.2	68.0 ±5.4	50.0 ±35.3	45.4 ±15.0	32.7 ±4.5	26.0 ±9.1	50.0 ±13.4	25.0 ±15.3	55.5 ±2.7	57.9 ±5.1	50.0 ±12.5	36.8 ±11.1
Host eggs/parasitized nest	9.2	7.2	6.7	5.0	5.4	8.3	7.6	2.5	8.0	7.4	7.4	3.9
Host eggs/unparasitized nest	9.4	8.3	9.0	7.5	8.6	10.1	9.0	6.1	9.3	8.8	9.0	6.3
Redhead eggs/parasitized nest	6.0	5.5	4.0	5.0	6.6	4.0	2.4	5.2	6.2	5.1	2.7	5.1
Host + redhead eggs/nest	12.5	10.2	9.4	9.6	10.5	12.0	9.2	6.7	12.4	10.7	9.2	7.8

[a] Search efforts in 1975 concentrated in hardstem bulrush cover type.

and highest in 1950 (71.4 percent). These years were also the years of lowest and highest number of nests found, respectively, which supports Olson's (1964) and Bellrose's (1976) contentions that the intensity of parasitism parallels that of normal nesting. Williams and Nelson (1943) found that only 6 percent of other species nests were parasitized by redheads.

Redheads generally laid fewer eggs per parasitized nest in 1974 (2.7 per nest). This was true for both mallards (4.0 per nest) and cinnamon teal (2.4 per nest). In 1975 there were more redhead eggs (5.1) per parasitized nest than host eggs (3.9). Some mallard and cinnamon teal hens were found incubating nests which contained all redhead eggs. Apparently the host eggs had been pushed out of the nest and into the water by the parasitic hens, and the hosts continued to incubate.

The number of host eggs per unparasitized nest was always found to be greater than the host eggs per parasitized nest. This supports Weller's (1959) contention that the presence of parasitic eggs stifles ovulation in the host.

The total number of eggs (host and redhead) per nest was greatest in 1950 for mallards (12.5) and in 1955 for cinnamon teal (12.0). This figure was lowest in 1974 for mallards (9.4) and in 1975 for teal (6.7).

Redhead parasitism did not seem to affect the nest success of the host species, as there is no significant difference between nest successes of parasitized and unparasitized nests (Table 7). The mallard nest success apparently did not change significantly in the four years of study.

The cinnamon teal success, however, seemed to be slightly higher in 1974. Weller (1959) also found that redhead parasitism did not affect mallard or cinnamon teal nest success.

The hatching success of mallard eggs, as well as redhead eggs in mallard nests, seemed to be highest in 1974 (64.5 percent and 33.3 percent, respectively). The teal hatching success was quite low in 1975 (21.8 percent), whereas the hatching of redhead eggs in teal nests was relatively high (9.5 percent). Williams and Nelson (1943) found that 24 percent of the redhead eggs and 96 percent of the host eggs hatched in parasitic nests. These figures were much higher than the ones for Knudson Marsh.

Other Bird Species

It appears that the numbers of mallard and cinnamon teal nests found on Knudson Marsh have decreased since 1950 (Table 7). The ruddy duck was also studied intensively in 1950 by Wingfield, but insufficient nests were found in later years to allow meaningful comparison.

Weller et al. (1958) reported that the number of Canada goose (*Branta canadensis*) nests found on Knudson Marsh decreased from the 146 and 144 found by C. S. Williams in 1940 and 1941 to 30 in 1950 and 25 in 1955. I estimated 100 pairs of geese nested on the marsh in 1975.

Wingfield (1951) found a small colony (65 nests) of great blue herons (*Ardea herodias*) in the upper marsh, as well as two smaller colonies composed of white-faced ibis (*Plegadis chihi*), snowy egret

(*Leucophoyx thula*) and black-crowned night heron (*Nycticorax nycticorax*) nests. No ibis or egret nests were found in 1955, but a few great blue heron and night heron nests were found on the upper and lower marsh, respectively.

A small colony of night herons nested on the upper marsh in 1974, and a small number of ibises, egrets and great blue herons nested on the lower marsh. A large colony of ibises (673 nests), along with scattered egrets and night herons, was found on the upper marsh in 1975, and 141 ibis nests and a number of great blue heron, night heron, and egret nests were found on the lower marsh. Apparently the ibis population of the area north of the Great Salt Lake varies from year to year in choice of a colonial nesting site (ibis data from D. E. Capen, personal communication).

DISCUSSION

This study has attempted to test the hypothesis that the redhead population of Knudson Marsh has declined due to changes in habitat. This hypothesis was not supported because no substantial change in redhead habitat was found between 1950 and 1975, yet the population has declined markedly during this period. These conclusions were derived from only four years of study over a 26 year period. It is now known that there were fewer redheads on the marsh at the time of this study than there were in the early 1950's; what fluctuations may have occurred between 1955 and 1974, however, are not known.

It is possible that the redhead population in 1950 was much higher than average, but the marsh is apparently capable of handling such a high density of nesting redheads. The reason for the drastic difference between the populations of 1950 and 1975, two years of similar habitat conditions, remains unknown. My opinion is that the difference is not related to the conditions at Knudson Marsh.

The marshes of the Great Salt Lake Basin, (including Knudson Marsh) are important as major redhead producing areas. The breeding population of this area (Great Basin population) is not as high as the population of the prairie parkland pothole region of the northern U. S. and southern Canada (prairie population). The nesting densities in the

Great Basin marshes are high (Bellrose 1976), however, and Knudson Marsh has a density of nesting redheads which is higher than that found in most wetland areas.

It seems logical that Knudson Marsh, being an area of prime redhead habitat, would have a breeding density which is higher than average. In years of a high Great Basin redhead population, areas such as Knudson Marsh may reach carrying capacity (which I assume is near the 1142 pairs per square kilometer found in 1950), and surplus redheads would nest in secondary and marginal habitat. When the redhead population is low, however, there would be no need to utilize marginal habitat if areas of primary habitat are not at their carrying capacity. Consequently, areas such as Knudson Marsh should be last to show a decrease in numbers during years of a low Great Basin population. The density of redheads on Knudson Marsh in 1975 was only 10 percent of the assumed carrying capacity, which would seem to indicate that either the Great Basin population of redheads has decreased from what it was in 1950, or that there was more primary habitat available in 1975 than in 1950, thus spreading out the breeding population.

Improvements in the form of state and federal wildlife refuges have taken place over the last 25 years in the Great Basin area. It is believed, however, that the total acreage of prime wetlands has not increased significantly, since there may have been an increase in wetland drainage and irrigation use of water supplies on private lands. It is unlikely, therefore, that the redheads moved to other marshes in the Great Basin that were not available in 1950.

Another explanation to a decrease at Knudson Marsh is a decrease in the Great Basin population. Such a population decrease could have come about in a number of ways. The redheads that once nested in Great Basin marshes may have shifted to another breeding area, such as the Canadian prairies. There may have been an increase in mortality, from hunting or other causes. It is also possible that a decrease in productivity has occurred due to behavioral or physiological changes.

Olson (1964) noted that the redhead is now a common nester in the prairie pothole region of Canada, but it was not abundant there in the early part of this century. Further investigation of the literature, however, reveals that insufficient data are available from the early 1900's and late 1800's to come to any valid conclusion regarding the abundance of redheads at that time. Weller (1964) postulated that redheads originated in the alkaline marshes of the southwestern United States and have only recently invaded the prairie pothole region. This may be an explanation for a decrease in the Great Basin population, but not necessarily so.

If redheads did leave the Great Basin and shift to the prairie region, we should have seen an increase in the prairie population over the past 25 years. Data supporting this, however, are lacking. It is believed by some authorities that the prairie redheads have decreased from the 1950's to the early 1970's. The U. S. Fish and Wildlife Service breeding ground survey did show a substantial increase in redheads for 1975, but this figure is imprecisely estimated for redheads. Survey estimates for the 1955-75 period do not indicate a trend.

Increased mortality is another possible reason for a decline in the numbers of redheads. Hochbaum (1946) reported that redheads in the Canadian prairie potholes were suffering a serious population decline despite excellent environmental conditions. He said it was "highly unlikely" that they moved elsewhere to breed, and that hunting pressure was probably a more likely explanation.

Geis and Crissey's (1969) study seemed to support Hochbaum's explanation. They determined that redhead and canvasback survival rates increased and mortality rates decreased during the closed seasons from 1960 to 1963. Rienecker (1968) however, found that the closed seasons did not seriously affect the mortality rates of California redheads. In addition, the continental redhead population has failed to show an increase, despite restrictive harvest regulations since 1960. It is doubtful, therefore, that an increase in hunting mortality is responsible for the decline in the numbers of redheads, and there are no data available to indicate a change in other types of mortality.

A third possible reason for a decrease in the Great Basin redhead population is a change in productivity. No significant decrease in productivity was noted at Knudson Marsh in this study. Weller (1959) noted a low productivity among redheads because of their "innately weak reproductive habits." They seem to desert nests more frequently than do other species, and lay many eggs in nests other than their own. Many of these eggs are never incubated and do not hatch. Consequently there is much fluctuation in the productivity of redheads.

Most redheads are semiparasitic, i.e., they lay eggs in other nests early in the nesting season when most other species are in the peak of nesting, then build their own nests and incubate later in the season (Weller 1959). In this respect, nest parasitism may be an added luxury which may or may not be beneficial to the population in a given year, but the late redhead nests will support the population in years of low production from parasitism. There may be years when a large number of young redheads are hatched parasitically, and the population will have a significant increase.

Another explanation for the perpetuation of a trait which is seemingly detrimental to the redhead's reproductive success is differential parasitic success. Although Weller (1959) found that nest parasitism was not beneficial, Olson (1964) found that redhead productivity was greatly increased by interspecific parasitism. Olson's study took place in southern Canada, where canvasbacks were the primary hosts. He found that parasitism was an effective method of avoiding competition between redheads and canvasbacks during years of limited resources. Because the canvasback is very similar and closely related to the redhead, it may be a better host than mallards and cinnamon teal, which serve as primary hosts in the Great Basin area. Consequently, redhead parasitism would be more successful in the prairie region than in the Great Basin, where canvasbacks rarely nest. Because there is considerable mixing of Great Basin and prairie redheads on the wintering grounds, however, isolation of one population segment does not occur (Weller 1964). In this way, the parasitic trait is perpetuated in the Great Basin redhead population, although it may not be beneficial to that population.

Sufficient data are not available to determine whether there has been a long term decrease in productivity. The apparent decrease shown for Knudson Marsh may not be significant. It is possible that there is much fluctuation in productivity as a result of the redhead's reproductive behavior and the population has not yet recovered from a downward trend. More research is needed in order to determine the effect of parasitism on productivity. It is not known if nest parasitism is a genetic trait, and very little is known about the survival and behavior of parasitic young.

I believe that the decrease in the number of nesting redheads on Knudson Marsh, despite the fact that no habitat change was found, indicates a decrease in the Great Basin population. This decrease is believed to have occurred largely as a result of productivity fluctuations. There may have been a long term shifting of redheads from the Great Basin population to the prairies, but there is no evidence to support this. Increased mortality is not believed to have been an important factor in the population decline.

Further research is needed on the effect of nest parasitism on redhead productivity, and on the survival and behavior of parasitically reared young. The status of redhead breeding habitat and breeding populations in the western U.S. needs to be assessed, and purchase and/or management of areas such as Knudson Marsh is highly recommended. More accurate data is needed on the present status and distribution of the continental redhead population.

SUMMARY

1. Redheads were studied on Knudson Marsh, Utah, during the breeding seasons of 1974 and 1975. This study was compared with earlier works by Wingfield (1951) and Weller et al. (1958) on the same area.
2. The study area is 70 hectares in size and is located in the Great Salt Lake Valley, where North America's greatest concentration of nesting redheads is found (Bellrose 1976).
3. The total marsh vegetation was systematically searched for nests in 1974; search efforts in 1975 were concentrated for the most part in the hardstem bulrush cover type.
4. Redhead, ruddy duck, mallard and cinnamon teal nests were marked and monitored, nest data were collected, and the fate of each nest was determined.
5. Habitat change was determined from a vegetation analysis conducted in 1974 by grid point sampling, and from cover maps made from aerial photographs.
6. Water conditions in the marsh were generally favorable in 1950 and 1975, and poor in 1955 and 1974.
7. No substantial change in the ratio of open water to emergent vegetation was detected. The ratio was 31:69 in 1950, and 38:62 in 1974.

8. The only major changes found in the species composition of the cover vegetation were a decrease in cattail from 12.4 percent to 2.0 percent and an increase in saltgrass from 6.5 percent to 18.6 percent. These two species were not found to be important as redhead nesting cover.

9. No significant change was found in the percent composition of hardstem bulrush, which was the preferred redhead nesting cover species.

10. During the two years of favorable conditions on the marsh, 1950 and 1975, the breeding population decreased from 500 to 50 pairs (90 percent decrease) and the number of nests decreased from 151 to 49 (67 percent decrease).

11. A decrease was also found in the two years of poor habitat conditions, 1955 and 1974, from a breeding population of 95 pairs to 50 pairs (47 percent decrease), and from 49 nests to 23 nests (50 percent decrease).

12. Hardstem bulrush was found to be the preferred cover type for redhead nests in the three years of study for which data was available: 1950, 1974, and 1975. This cover type composed less than 60 percent of the total marsh vegetation, yet 75, 70 and 90 percent, respectively, of the redhead nests found were in this cover type.

13. Redhead nests were constructed at a greater distance from open water in 1950 than in the present study, when there was less

competition for nest sites close to open water because of the lower density of nesting birds.

14. No significant difference was found between the average redhead clutch sizes for 1950, 1974 and 1975 due to the high variation in number of eggs per nest.

15. Nesting success in redhead nests which were active when found was greater in the present study than in 1950, although the success of all nests of known fate was unchanged.

16. Predation was higher in 1950 (24.6 percent of total nests preyed upon) than in the present study, when it was a very minor factor in nest success.

17. Hatching success in successful nests was significantly higher in 1950 (72.8 percent) than in the present study (61.0 percent and 37.3 percent).

18. Redhead productivity, both in terms of eggs hatched per hectare and eggs hatched per nesting effort, showed a decline from 1950 to the present study, although the latter comparison may not be significant.

19. Mallards and cinnamon teal were the primary hosts for redhead interspecific parasitism, which seemed to parallel normal nesting. The highest percentage of nests parasitized was in 1950 (the year of maximum redhead nesting) when 71.4 percent of the host nests were parasitized. In 1974, the year of lowest parasitism (and redhead nesting), 36.2 percent of the nests were parasitized.

20. Redhead parasitism was not found to affect the nest success of the host species.

21. There seemed to be fewer mallards, cinnamon teal and ruddy ducks nesting on Knudson Marsh in the present study than in earlier ones. Canada geese and colonial nesting birds, however, seemed to have increased on the marsh.

22. The decreases shown in the redhead population of Knudson Marsh were not found to have been related to changes in habitat.

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APPENDIX

Table 8. Plant species present on Knudson Marsh, Utah, 1974 (names from Holgren and Reveal 1966).

Scientific name	Common name
Amaranthus sp.	Amaranth
Apocynum cannabinum L.	Dogbane
Asclepias incarnata L.	Swamp Milkweed
Chenopodium album L.	Lambsquarters
Cyperus sp.	Flatsedge
Distichlis spicata L.	Desert Saltgrass
Eleocharis macrostachya Britton	Common Spike-rush
Helianthus annuus L.	Sunflower
Hordeum jubatum L.	Foxtail Barley
Lemna minor L.	Common Duckweed
Monolepis nuttalliana (Schult.) Green	Monolepis
Phragmites australis (Cav.) Trin. x Steud.[a]	Cane
Polygonum persicaria L.	Smartweed
Polypogon monspeliensis (L.) Desf.	Rabbitfoot Grass
Pot amogeton pectinatus L.	Fennelleaf Pondweed
Ruppia maritima L.	Widgeongrass
Salicornia europaea L. ssp. rubra (A. Nels.) Breitung	Glasswort
Scirpus acutus Muhl.	Hardstem Bulrush
Scirpus olneyi A. Gray	Olney Bulrush
Senecio hydrophilus Nutt.	Water Groundsel
Solanum dulcamara L.	Nightshade
Triglochin maritima L.	Shore Arrowgrass
Typha latifolia L.	Common Cattail
Xanthium strumarium L.	Cocklebur

[a] Phragmites communis Trin. in Holmgren and Reveal (1966).

VITA

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Candidate for the Degree of

Master of Science

Thesis: Nesting Ecology of the Redhead Duck on Knudson Marsh, Utah

Major Field: Wildlife Science

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